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THE

AMERICAN NATURALIST

VOL. XXXIII. *November, 1899.* NO. 395.

THE WINGS OF INSECTS.

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CHAPTER V.

The Development of Wings.

I. FIRST APPEARANCE, POSITION, AND GROWTH OF WINGS.

THE development of wings is one of the many subjects of biologic study which have been first undertaken in their more difficult phases. The internal processes concerned in the making of an insect wing were first studied by Weismann in the Diptera,[1] and in those Diptera in which conditions are most difficult of interpretation. One by one forms of less complexity have been studied, and a rational account of the process of wing development has at length found its way into several textbooks. The process is still most fully illustrated, however, by studies of representatives of the two groups which are least typical for insects as a whole, the Diptera and the Lepidoptera. Rehberg's inconclusive paper on wing development in *Blatta*

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[1] Weismann, A. *Zeit. wiss. Zool.*, vol. xiv (1864), pp. 187–336.

germanica[1] remains the only considerable attempt to study the making of the wing in an insect with incomplete metamorphosis. In this chapter we give the results of some studies in which we have endeavored to follow the phylogenetic order of wing development.

It is not necessary to trace in this place the steps by which the present state of knowledge of wing development has been reached; for this has been well done by several writers. Among the more complete of these summaries are those of Gonin[2] and of Pratt.[3]

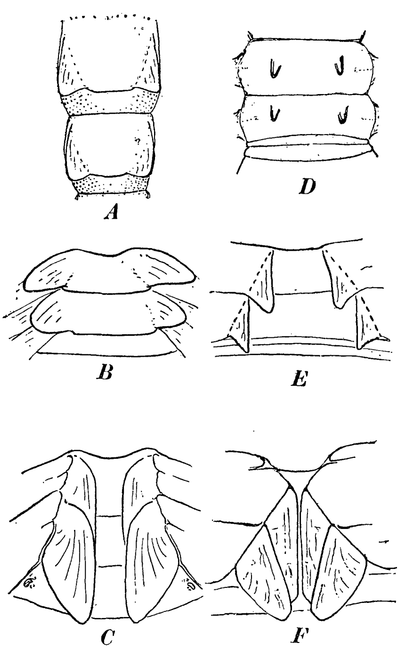

FIG. 82. — Wings of nymphs: *A*, of a stone fly (Capnia); *B* and *C*, of a grasshopper; *D*, *E*, and *F*, of a dragon-fly. In the four lower figures the dorsal half of the body of the nymph is represented as spread out flat. Figures *B* and *E* are from nymphs one third grown; and *C* and *F* from nymphs that were three fifths grown.

Neither does it seem desirable to enter into a detailed discussion of controverted points, our object being merely to state what is definitely known on this subject, and to add the results of some of our own investigations.

It is well known that the wings of insects arise as sac-like folds of the body wall of the second and third thoracic segments. These folds first appear at the point where the suture between the tergum and the pleurum later develops. In most insects with incomplete metamorphosis they are so directly continuous with the tergum and become so solidly chitinized with it that they have generally been interpreted as outgrowths from its caudo-lateral margin (Fig. 82, *A*, *B*).

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[1] Rehberg, A. *Jahrb. d. k. Gymn. zu Marienwerder*, 1886.

[2] *Bull. de la Soc. Vaud. des Sci. Nat.*, vol. xxi, pp. 90–98.

[3] *Psyche*, vol. viii (1897), pp. 15–30.

In the Plecoptera, Ephemerida, Hemiptera, Blattidæ, *et al.*, the external changes during growth are comparatively slight—increase in size and internal differentiation, and the development of the veins and of the basal articulations. In the more specialized Orthoptera there occurs the well-known reversal of position of the wings at the last molt. In the Odonata there are the noteworthy differences that the wings arise in an erect position upon the body wall, and at midway the length of their respective segments, and not from the hind margin (Fig. 82, *D*). They appear at a time when the tergum and the pleura are very little chitinized, and are hardly more identified with one than with the other. Later, as in the saltatorial Orthoptera, owing to a rapid growth of the pleura, especially at the wing bases, they are pushed over upon the dorsum and lie in an inverted position (Fig. 82, *E*, *F*), to be righted only at the final transformation.

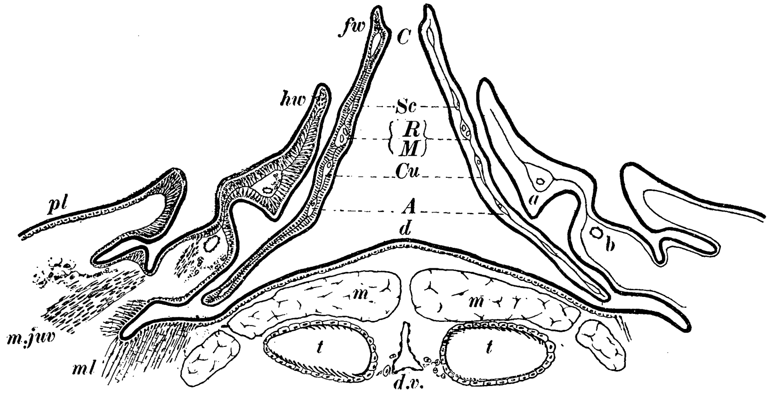

FIG. 83. — Dorsal part of a transverse section of a nymph of *Celithemis elisa*, one third grown: *d*, dorsum; *pl*, pleurum; *d.v.*, dorsal vessel; *t*, *t*, tracheæ; *m*, *m*, muscles in cross-section; *ml*, muscles in longitudinal section; *m.juv*, developing muscle of the wing; *hw*, hind wing; *fw*, fore wing; *a* and *b*, the cut ends of the basal transverse trachea of the hind wing; *C*, costa; *Sc*, subcosta; *RM*, the coalesced radius and media; *Cu*, cubitus; *A*, anal vein.

Fig. 83 shows the relations of parts in a dragon-fly nymph one third grown. It represents a partial cross-section passing through the posterior part of the basal attachments of the hind wings and through the fore wings just before the arculus. In the hind wings are seen (*a*, *b*) the cut ends of the transverse basal trachea. In the fore wings the tracheæ in the vein cavities are seen in section. The pleura (*pl*) are seen overlying the bases of the wings.

It is interesting to follow the basement membrane of the hypodermis throughout the section, noting how the hypodermal cells are elongated in certain parts, rounding out the sharp angles of the exterior, and completely occupying the narrower spaces in the wings.

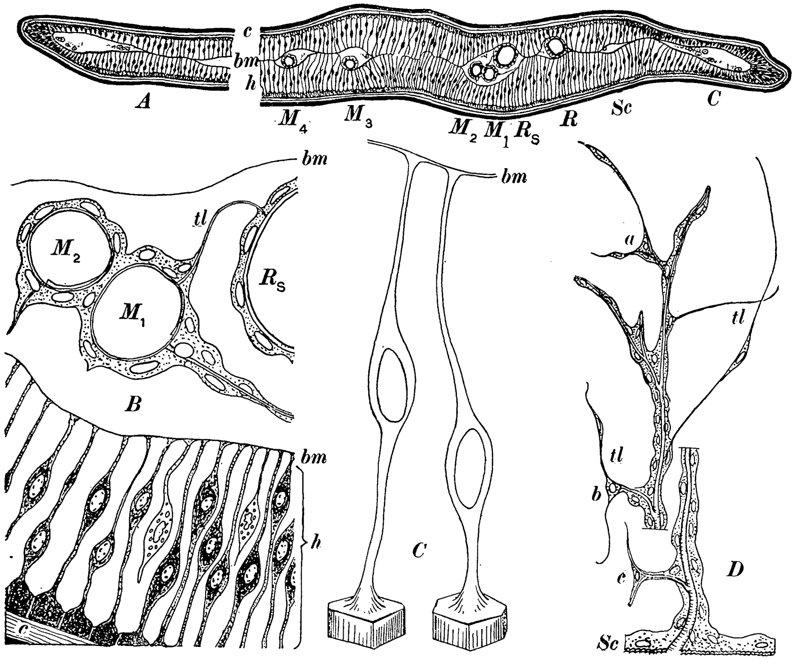

FIG. 84.—*A*, cross-section of a fore wing (in part omitted) of a nymph, two thirds grown, and recently molted, of *Anax junius*; *c*, cuticle; *bm*, basement membrane; *h*, hypodermis; the veins of the wing are designated by the usual lettering. *B*, a small portion of the same, more highly magnified; *tl*, tracheole; *C*, two hypodermal cells from the same; *D*, base and apex of the fifth antecubital trachea, as seen in horizontal section, of another wing of the same specimen; *Sc*, epithelium and intima of one side of subcostal trachea; *a*, *b*, *c*, cells at origin of tracheoles; *tl*, *tl*, tracheoles.

It is also important to note that the basement membrane of the hypodermis of the wing differs in no respect from that of the hypodermis of the body wall, and is continuous with it. In the thinner parts of the wing the two basement membranes meet and fuse, thus forming what has been termed the middle membrane of the wing. Along certain lines, seen in section in the figure, the two membranes remain separate, and thus are formed the cavities of the wing-veins.

Fig. 84 represents a partial section of a fore wing of a nymph of *Anax junius* two thirds grown; the section was taken at the nodus. The general features here seen are common to the wings of all nymphs — two layers of very elongate, hypodermal cells, which meet in places and form the middle membrane, and remain separate in other places, forming the vein cavities, which usually contain tracheæ. At *B* and *C* in the figure is shown the character of the commoner hypodermal cells.

There is in insects with a complete metamorphosis another type of wing development; this is so different in its external aspects that it may best be described, with respect to these, separately, after which the common fundamental features of wings may be considered.

It has been abundantly shown by others that modification of the type of wing development has kept pace with the increasing complexity of the metamorphosis. The wing-buds are most erratic in the headless, appendageless larvæ of the higher Diptera, Hymenoptera, etc., while they are simplest in larvæ possessing a head, legs, and mouth parts, and especially in those in which the structure is altered least in transforming to imagoes. Among coleopterous larvæ are some in which, save for the appearance of wings, the change is slight; and, indeed, in certain of these (notably the meal worm) specimens are occasionally found with the wings developing externally.

A little coccinellid beetle (*Hippodamia 13-punctata*) has furnished us simpler and more instructive conditions of wing development with complete metamorphosis than have heretofore been fully presented. Fig. 85 shows three early stages in the development of the wings of this insect. Each wing begins as a disk-shaped thickening of the hypodermis (Fig. 85, *A*), which was first observed when the larva was about one fifth grown. A prominent spine, which stands at its dorsal margin, is an excellent landmark to aid in finding it at the first, and when found it is certainly recognized by a slightly concentric arrangement of its cells. It is not at first in connection with nor in approximation to any trachea. The disk elongates and then becomes folded upon itself, thus initiating the wing surfaces. At the time of the folding the wing retreats from the surface, settling down into a pouch-like invagination of the hypodermis (Fig. 85, *C*). Thus it approaches a lateral tracheal trunk, from one of whose smaller branches a few small tracheoles now enter it. As growth continues, the wing extends itself slowly ventrally, as shown in Fig. 86; the mouth of its enveloping pouch becomes somewhat closed by the growth and extension of the pleural hypodermis, but to very various degrees in different specimens, a large part of the larval wing being often found covered exteriorly only by the chitine of the integument.

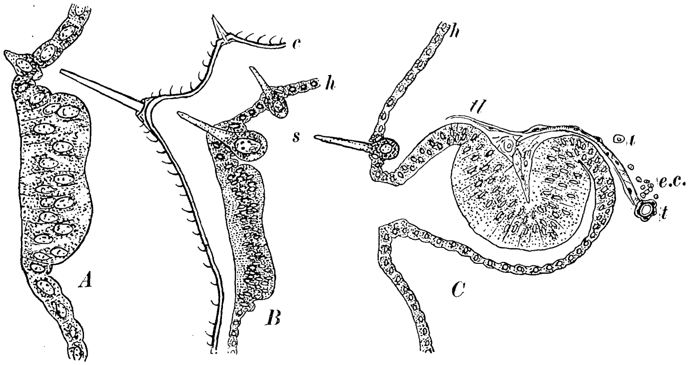

FIG. 85.—Three stages in the early development of wings in *Hippodamia 13-punctata*: *A*, from a larva about one fifth grown; *B* and *C*, from older larvæ, less magnified; *c*, loose cuticle, shown only in *B*; *h*, hypodermis; *s*, spine; *t*, trachea; *tl*, tracheole; *l*, leucocyte; *e.c.*, embryonic cells.

During the last larval stage the wing is pushed outward and the fold of hypodermis overlying its edges is withdrawn radially, and it emerges from its pouch, becoming greatly extended ventrally under the old larval cuticle, with its walls thrown into numerous folds. When the last larval skin is shed, a still greater expansion transforms it into a wing of the pupa.

Previous to their emergence from the larval wing pockets, there is no appreciable difference between the fore and the hind wings; after this, however, the elytron shows a distinctly thicker layer of hypodermis on its dorsal side, and the thinness of the hind wings steadily increases with their expansion in area. The hind wings are greatly expanded at the final transformation, while the elytra are almost as large in the pupa as in the imago.

Comparing now the two types of wing development (external and internal), we see that, despite great superficial differences, there are important common features. In both cases the wings arise in early life and form a double plate-like fold of hypodermis, between whose layers tracheæ shortly penetrate. In the former the extension of the wings is gradual and moderate, excepting at the time of transformation; in the latter they early settle down into deep hypodermal pockets, in which their extension is of necessity retarded, although cell multiplication seems not to be.

The principal structural elements which enter into the making of the insect wing are hypodermis, tracheæ, nerves (which, though always mentioned and once or twice figured by other students, we have rarely seen in wings), leucocytes, embryonic cells, and, possibly, sometimes fat cells. Of these, the first two only are essential structures; and these are so important as to merit special treatment.

II. The Origin of the Tracheation of the Wing.

In wings developing externally like those of a dragon-fly one sees the principal tracheæ passing very early out into the wing-bud, branching freely and forming by multitudinous terminal anastomoses a network of capillary tracheoles. In a horizontal section of a nymphal wing one may see how the branches of the tracheæ are formed. Fig. 84, *D*, is from such a section. It will be observed that the terminal tracheoles are intracellular, the tracheæ intercellular; but that there is easy transition from one condition to the other.[1]

In a wing so mounted that the tracheal system is filled with air it is easy to see everywhere anastomoses between the distal ends of the tracheoles. This is not shown in our figure; indeed, it is difficult to see it in sections anywhere. The walls of the tracheoles are of extreme tenuity; the best of chitine stains leave them untouched; they are probably protoplasmic tubes at their extremities, such as would best subserve the respiratory process. Tracheoles of this type are everywhere relatively short.

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[1] There are no such distinct transition cells between tracheæ and tracheoles as Holmgren found (*Anat. Anz.*, vol. xi, pp. 340–346) in the spinning glands of caterpillars, although the cells at *a*, *b*, *c* might seem to stand in the same relation.

In the much discussed tracheation of the lepidopterous larval wing there are the two well-known systems: the temporary system of tracheoles, which enter the wing in the penultimate larval stage and which are functional in the last larval stage; and the permanent wing tracheæ, which grow out into the wings in the last larval stage, but do not become functional until pupation, when they have acquired terminal and lateral tracheoles of their own. In each case the developing air-vessels arise from the epithelium of the lateral tracheal trunk; but they do not communicate with the lumen of this trachea

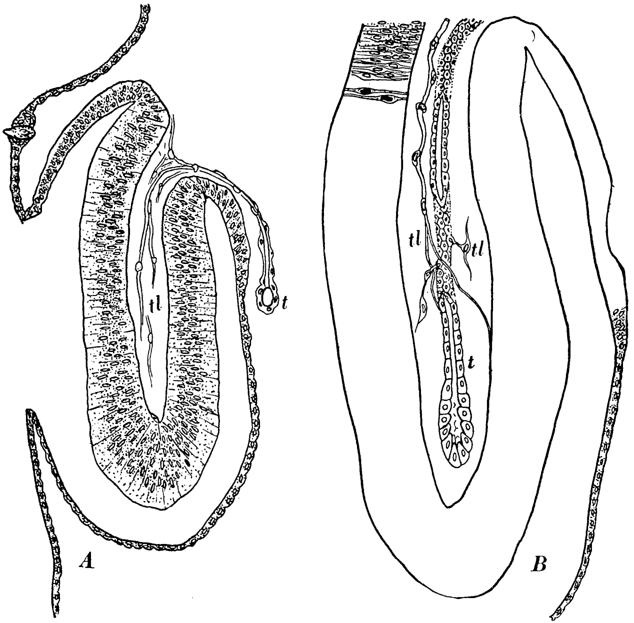

Fig. 86. — Wings of *Hippodamia 13-punctata*, two stages later than those shown in Fig. 85: *t*, *t*, tracheæ; *tl*, *tl*, tracheoles.

till after a molt, their mouths being closed at first by the preexisting intima of this trachea. Fig. 86, *B*, will show clearly that in beetles we have the same conditions, though here the temporary system is much less highly developed. This is from a well-grown larva; *tl* is a tracheole; only such are present in the younger wing shown at *A* in this figure; *t* is a developing trachea; and *tl*, *tl* are developing tracheoles attached to single cells of the wall of the trachea.

We believe that this peculiar temporary system of tracheoles is due to and dependent upon the retention of the wing within the narrow limits of its hypodermal pouch; for its small size alone renders its aëration by simple tracheoles possible. We believe that this also explains the retarded development of the tracheæ. In an externally developing wing it is necessary that the tracheæ should grow with the wing, in order to carry the tracheoles out within reach of the tissues; but when a wing develops internally its length for a long time does not exceed the length of normal tracheoles. In such a wing the tracheæ develop only when needed — at the approach of the time when rapid extension is to take place.

III. The Behavior of the Hypodermis.

The cells of the hypodermis are remarkable, not only for their secretory and excretory activity, but also for their capacity for rapid shifting and readjustment. Their life history is one of alternating conditions: first, growth beneath a limiting layer of chitine; then, sudden lateral extension when the chitine is thrown off at molting.

The typical hypodermis of prismatic hexagonal cells is found only where the body wall is smooth; in short curves and angles, and in folds of the integument, and in the wings where close crowding is followed by enormous expansion their change of form is very great. At their ends, however, these cells maintain fairly constant relations. Externally they must needs cover the surface to provide its integument, internally they join the basement membrane; between these two planes, however, they may assume almost any shape, according to the conditions of their growth. Their commoner forms are shown in the figures presented herewith.

The basement membrane consists, we believe, of the fused inner ends of the hypodermal cells or of processes from them. It is often incomplete or fenestrated, and it is of extreme tenuity. Semper thought it (in the Lepidoptera) composed of leucocytes applied to the free inner ends of the hypodermal cells, and his opinion has been concurred in by several subsequent investigators; but we are inclined to believe that in the forms we have studied, the formation of it from leucocytes is at least exceptional, for the following considerations: —

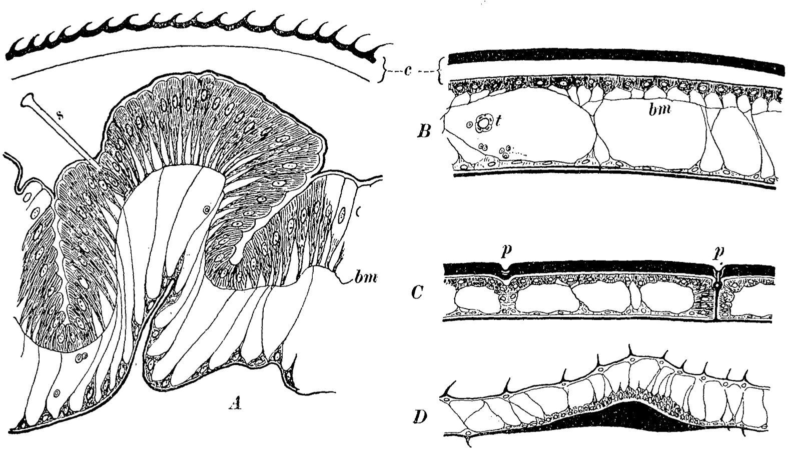

Fig. 87. — Sections of wings of *Hippodamia 13-punctata*, all drawn to the same scale: *A*, from full-grown quiescent larva, a bit of the wing crumpled under the loose larval cuticle; *s*, a deciduous spinule; *bm*, basement membrane; *B*, fore wing (elytron) of an old pupa; *C*, fore wing of a newly transformed imago; *p*, pits above the chitinous pillars; *D*, hind wing of a newly transformed imago, showing especially the manner of formation of a special chitinous brace.

1. While leucocytes are not infrequently seen lying against it, we have seen no direct evidence of their participation in its development.

2. During early stages it is well formed and *destitute of nuclei*.

3. In later stages, when, after the expansion of the wing, it contains distinct nuclei, there is evidence that some of these at least are derived from the hypoderm cells whose nuclei, once crowded up to this level, have remained stranded there after the expansion of the wing.

In past accounts of hypodermal development in wings too little attention has been paid to the mechanics of the developmental process—to the varied conditions under which the cells labor in successive stages. To these conditions are mainly due the different cell forms seen; and, except where like conditions are compared, different series will be contradictory. A study of hypodermal ontogeny in the wings of representatives of half a dozen orders of insects convinces us that it is impossible to summarize the process except in the most general terms.

In very early stages in externally developing wings there is found a condition of the hypodermis not far removed from the normal. The cells are only a little less prismatic, a little more columnar or rhomboidal, and the two layers meet internally in very limited tracts. Fig. 89, *A*, is from the wing of a young acridid nymph. It would answer almost equally well for a young nymph of the dragon-fly, Gomphus, or for several ephemerids we have studied; or, for that matter, for parts of the ephemerid tracheal gill or for its operculum; or, save for the lack of tracheæ, for the overlapping edge of the prothorax or for a section of the labium.

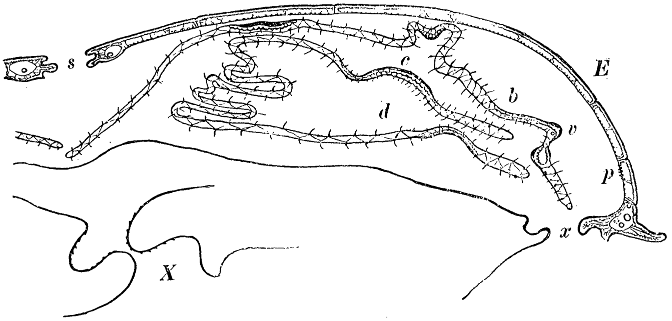

FIG. 88. — Cross-section of wings of a newly transformed imago of *Hippodamia 13-punctata, in situ*: *E*, fore wing; *b*, basal portion of hind wing; *d*, distal, reflexed portion of hind wing; *s*, elytral suture; *v*, a vein; *c*, a cuticular thickening; *p*, stridulating (?) processes; *x*, the interlocking ridges, seen more magnified at *X*.

This early condition is followed by a long period of growth, during which the hypodermal cells become crowded and much more elongated, their nuclei, which were originally nearer their inner ends, coming to occupy a spindle-shaped middle portion in the cells (Fig. 84). The crowding is excessive, and the effect of it in massing the cells much more marked, of course, when wings are developed internally. But even here the spindle-form cell is recognizable (Fig. 86, *B*), and all the cells appear still to extend from surface to surface of the hypodermis.

The first great expansion of the wing occurs just before pupation, with insects having complete metamorphosis, but not until the final transformation, with those in which the metamorphosis is incomplete. This expansion results in the broadening of the bases of the hypodermal cells, in the settling down of their nuclei close upon the chitine layer, and in the drawing out of their inner ends into a long, slender prolongation, which generally retains its attachment to the basement membrane, and thus to its neighbors opposite, in those portions of the wings where the membranes are united. The cells thus become peaked in appearance. Their breadth and height will depend, however, on (1) the extent of the previous crowding; (2) the extent of the surface they are now called upon to cover; and (3) the width of the space they are now called upon to bridge. When, through excessive crowding, some of the innermost

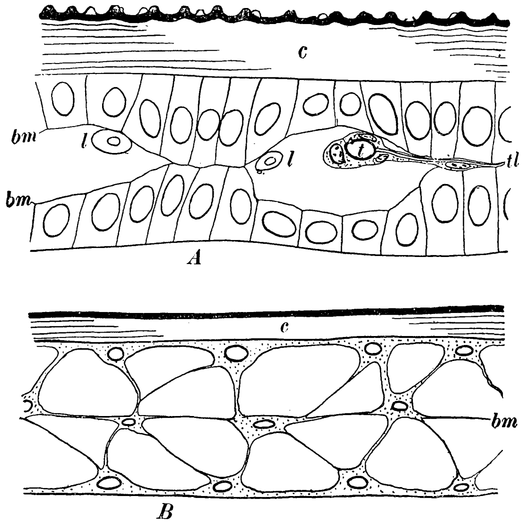

FIG. 89. — *A*, cross-section of the wing of a young acridid nymph : *c*, cuticle ; *bm*, *bm*, basement membrane ; *t*, trachea ; *tl*, tracheole ; *l*, leucocyte ; *B*, stellate cells in hypodermis, from the anal angle of a wing shown in Fig. 83.

nuclei have come into contact with the basement membrane at the subsequent expansion of the wing, these, instead of retreating with their fellows to the chitine layer, seem instead to remain where they are, and to attract to themselves the slender prolongations of the neighboring cells. They thus acquire a stellate appearance, as shown in Figs. 89, *B*, and 90, *D*. These seem to occur only in narrow spaces, in which great expansion has followed close crowding.[1] We have found them in Leucorhinia (Fig. 83) in the rapidly expanding anal angle of a wing, the greater part of which appeared as Fig. 84, *B*, the cells having spindle-shaped bodies. We have seen them also in the anal angle of the wing of a pupa of Corydalis, the pre-anal area being filled with the peaked cells more characteristic of that stage.

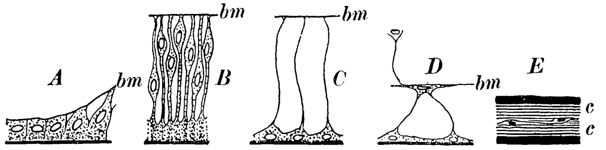

FIG. 90. — Diagram illustrating the behavior of the hypodermis during the development of an insect wing: *A*, nearly normal hypodermis; *B*, the same, after being crowded within the wing fold; *C*, the same after the first great expansion of the wing; *D*, a cell stranded upon the basement membrane; *E*, disappearance of the hypodermal cells with chitine formation.

The segregation of the hypodermis, which results in the accumulation of it around the tracheal channels and in those parts of the wing to be made strong by heavy deposits of chitine, takes place during the final stages. Some interesting illustrations of it are shown in Figs. 87 and 88, and are explained in the legends to the figures. These processes and the final disappearance of the scattered hypodermal cells, wasting themselves away in chitine formation, are the final steps in the making of the wing.

The accompanying diagram (Fig. 90) will, therefore, represent what we think may fairly be taken as typical for the behavior of the hypodermis. While this strongly suggests ontogeny, we desire explicitly to state that we believe these changes to accompany certain conditions under which cells are placed, rather than any particular stages.

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[1] This is the "Grundmembrane" of Semper, which was believed by him to be formed by leucocytes during the pupal period, and, therefore, to be distinct from the middle membrane of the wing of the larva.

IV. THE TRACHEÆ AND THE HYPODERMIS.

After discussing these two separately, there remain a few interesting features of their correlated behavior to be noticed.

In all insect wings the two plates of hypodermis constituting the wing fold are at first separate, *i.e.*, not fused internally. At the time when the tracheæ enter the fold the two layers become approximated along lines midway between the tracheæ, resulting in actual fusion of the internal ends of the cells. We have already shown in Psocus[1] (and have seen in several other insects) the external evidences of the gradual lateral extension of the fused area to delimit definitely the channel through which the tracheæ pass. The term "cuticular thickenings" has been used hitherto to designate the pale bands along the tracheæ, and the veins to be formed here will be, of course, cuticular thickenings; but until the veins are formed (and this does not occur until the final molting) the term is inaccurate and misleading. A glance at Fig. 84, *A*, will discover that the hypodermis is in the earlier stages actually thinner here than elsewhere. It is only at transformation to the imago that the cells become aggregated about these channels and form there the dense chitine of the veins. The pale color of the bands, indicating the extent of the vein cavities when viewed by transmitted light, is doubtless due to the fact that the hæmolymph filling these cavities is more translucent than the hypodermal tissue which completely fills the wing elsewhere.

But, returning to the earlier stages, we have seen that, in wings developing externally, the hypodermis encloses the tracheæ in channels which ultimately become veins. It is now to be noted that there are often channels present which do not contain tracheæ. This is oftenest true of two large channels at the lateral margins of the wing (Fig. 84, *A*). Of these the costal remains abundantly lined with cells, which ultimately form the strong costal vein. Its trachea is often atrophied, probably owing to the disadvantageous position of its base in relation to air supply, as we have hitherto indicated. The anal channel becomes obliterated, and the dense hypodermis of its walls dispersed by subsequent expansion of this part of the wing. In some wings in which this space persists, as in Psocus, it is occupied by the third anal trachea.

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[1] *American Naturalist*, vol. xxxii, p. 241, Figs. 11, 12.

In wings developing within small hypodermal pockets, while the cells are densely crowded and while the fusion of the cells internally joining the two layers is more tardy and incomplete, the same principal channels are formed. In the Lepidoptera, though the development of their tracheæ is retarded, the temporary tracheoles pass out in tangled skeins through the original channels.

But the process of reduction of tracheæ, already begun in the lower orders, finds favorable conditions for progress in the shorter and more open wing sacs developed internally; and we find in all but the more generalized members of certain orders that the close correspondence between tracheæ and channels due to simultaneous development is again lost. Illustrations have been abundantly offered in preceding chapters; we are here offering only a suggestion as to the reason, first for this correspondence, and then for the loss of it. While the tracheæ seem at first to have been the determining factor in the venation, and while we have been able to show a gratifyingly large number of cases in which the tracheæ show the unmistakable signs of homology, and cases in which the course of the veins is still determined by them, it appears that in certain insects the tendency of the hypodermis to segregate itself and to form chitine along certain lines has become so well established as to be more or less completely independent of the tracheæ. The veins have to do in these cases with locomotion in adult life; the tracheæ, with growth and metamorphosis. The adult wing, whatever it may have been originally, has become a dry resilient plate of chitine traversed by finely adjusted supports. It would be manifestly disadvantageous for the tracheæ to follow the course of these supports, sharp angled, and often recurrent; but in wings with slight fusion between the walls this is unnecessary. The disappearance of distinct tracheal channels has restored open competition between the tracheæ, which accounts for the more rapid disappearance of all save those most favorably situated in relation to the source of the air supply — usually only two in the most specialized insects, which still stand as representatives of the two groups of tracheæ with which we begin our series.

Fortunately for the study of homologies in insect wings, the veins had attained an arrangement so useful that it could be held by natural selection after the tracheæ had ceased to determine their position.